

## Aspects of life history of *Platynemesis subdilatata* (Zygoptera: Platynemididae) in Northeast Algeria

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(Received 18 April 2015; accepted 20 August 2015)

The determination of seasonal regulation is important to understand how species have adapted to their local environmental conditions. In this study, we investigate the life history of a North African endemic damselfly, *Platynemesis subdilatata*, in a northeast Algerian population. We combined field and laboratory investigations to assess the embryonic development, larval growth, emergence pattern and adult flight season. The embryonic development was direct and asynchronous, with 50% of all eggs hatching after three weeks of egg laying and a hatching period ranging from 13 to 51 days. Hatching success was 48.8%, and the causes of hatching failure were infertility and unhatchability. Larval population structure was quite asynchronous during the winter and less so before emergence. The occurrence of larval diapause is improbable due to the increase of the proportion of the last larval stadium in late winter. Emergence was asynchronous with half of the larval population (EM50) emerging after 44 days within an emergence season of 122 days. Sex ratio at emergence was slightly female biased (50.6%). The flight season lasted 133 days starting from early May. The species reached its sexual maturity after six and seven days of emergence in male and female, respectively. Lifespan was not significantly different between sexes with a mean of  $7.75 \pm 6.45$  days ( $\pm$  SD). Our results suggest that the species is univoltine with a typical summer species life history.

**Keywords:** Odonata; damselfly; seasonal regulation; embryonic development; larval growth; emergence; exuviae; body size; *Platynemesis subdilatata*; Algeria

### Introduction

In temperate zones, development is constrained by low winter temperatures in the north and by summer drought in the south. These time stressors (induced by seasonality) shape the life history and determine seasonal regulation of species (Stoks, Johansson, & De Block, 2008). Corbet (2003) discussed three dominant patterns of seasonal regulation in temperate odonates. First, spring species synchronize their development, enter larval diapause at the final larval stadium in the winter and have short emergence season. Second, summer species do not have synchronized development, thus overwinter at different larval stadia and consequently display a long asynchronous emergence. These two categories are common at high latitudes, but Paulson & Jenner

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(1971) pointed out that there is a wide range of intermediate life histories at low latitudes. The third category encompasses typically obligatorily univoltine summer species which overwinter as diapausing eggs (e.g. Boehms, 1971; Sawchyn & Gillott, 1974; Śniegula, Drobnik, Gołab, & Johansson, 2014; Śniegula & Johansson, 2010; Tai, 1967). Unfortunately, most studies in temperate regions on voltinism and seasonal regulation have been carried out in relatively cold high latitudes (Corbet, Suhling, & Soendgerath, 2006), but data from southern areas where drought is common and the mean annual temperature is considerably higher are scarce (Ferrerias-Romero, Atienzar, & Corbet, 2000; Jödicke & Thomas, 1993).

Besides temperature, the type of habitat, i.e. stagnant versus lotic water, is also important in determining the life history of a species because both types of habitats have different abiotic and biotic properties (Corbet et al., 2006). Usually, species that inhabit stagnant water produce more generations per year than those living in lotic water. Groups of odonates that are intimately linked to lotic water in temperate zones are Gomphidae, Calopterygidae, and Platycnemididae, and most of their representatives are univoltine, semivoltine, and even partivoltine (Corbet et al., 2006). Recently, a partially bivoltine population of the stream-dwelling *Coenagrion mercuriale* was observed in the southern range limit (northeast Algeria) with no apparent winter diapause (Mahdjoub et al., 2014). However, in the same region and at about the same elevation, a univoltine population of *Gomphus lucasii* (Zebba, Khelifa, & Kahelerras, accepted a) and a partially semivoltine population of *Onychogomphus costae* were recorded (Zebba, Khelifa, & Kahelerras, accepted b); both showing no apparent larval development during the winter. These findings show that voltinism and the occurrence of larval diapause in lotic species of hot temperate areas are quite variable.

There is a large literature that shows that body size of exuviae and adults decreases over the season (Banks & Thompson, 1985; Mahdjoub, Khelifa, Zebba, Bouslama, & Houhamdi, 2015; Michiels & Dhondt, 1989; Purse & Thompson, 2003). Vannote & Sweeney (1980) explained the seasonal decline in body size as a response to environmental conditions. That is, individuals that emerge late in the season experience higher temperatures than those emerging earlier, yielding faster development rate and reduced body size in the former. On the other hand, a hypothesis of Rowe & Ludwig (1991) stated that there might be a tradeoff between age and reproductive time. In other words, it is more advantageous to emerge early with a smaller size rather than spending more time growing as larva, because it is costly for individuals to emerge late due to shorter reproductive period.

In this study, we investigate the life cycle of *Platycnemis subdilatata* (Platycnemididae) in northeast Algeria; this species has not been studied before. It is a medium-sized damselfly, endemic to North Africa (Morocco, Algeria, and Tunisia) (Dijkstra & Lewington, 2007), and widely common in streams and rivers. Combining field and laboratory studies, we aim to explore the embryonic development time, larval growth, and temporal pattern of emergence of the species in a northeastern Algerian natural population. In addition, we investigate the seasonal pattern of body size during the emergence season based on exuvia measurements.

## Material and methods

### Study site

We conducted this study in a shallow stream, located 6 km east of Guelma city, northeast Algeria (36°27'24.50"N, 7°30'29.53"E). The watercourse was about 5 m width, 0.4 m depth, with velocity of about 0.35 m s<sup>-1</sup>. The bottom substrate was mainly silt with some sand and gravel. Most of the stream was shaded by tall trees of *Salix pedicellata*, *Populus alba* and *Eucalyptus globulus*. The banks had relatively dense stands of *Typha angustifolia*, *Apium nodiflorum*, and *Nasturtium officinale*. The Odonata community that lived in the stream consisted of *Gomphus lucasii*, *Orthetrum coerulescens*, *Calopteryx haemorrhoidalis*, and *P. subdilatata*.

### ***Embryonic development***

In order to get eggs from natural oviposition, stems of fresh lesser bulrush (*Typha angustifolia*) that did not contain eggs were placed on the water surface, next to reproductive sites. To make sure that only one female oviposited in the substrate we gently chased other breeding pairs that landed on the support with a stick. The experiment was conducted when air temperature was between 26 and 27°C to avoid any effect of temperature on subsequent embryonic development. After oviposition, our artificial oviposition sites were taken to the laboratory and parts of the stems containing eggs were then placed in rectangular containers (10 × 5 × 3 cm<sup>3</sup>) filled with aged tap water and put under natural light conditions. We recorded air temperature in the laboratory with an electronic thermometer to the nearest 0.1°C three times a day (at 09:00, 14:00 and 20:00). Water was replaced three times a week to avoid algae growth. The hatching of eggs was checked daily. After hatching, larvae were placed in other containers, counted and returned to their original site.

### ***Exuviae collections***

Field visits started in mid April 2012 and ended when no exuviae were observed. From 25 April to 28 July visits were conducted daily, but every three days later on. We selected three stretches of 20 m where exuviae were searched for thoroughly in the late afternoon. After each exuviae collection, no exuviae were left in the study site. The trampling effect on bank vegetation was reduced by walking through the same path each visit. Exuviae were taken to the laboratory for sex identification and measurements. Exuvia body length and head width were measured to the nearest 0.01 mm with a digital caliper. The time after which half of the population emerges (EM50) was calculated for both sexes. Sex ratio at emergence was also estimated as the percentage of females with respect to all exuviae.

### ***Larva collections***

From December 2011 to July 2012, larvae were collected monthly (in the last week of the month) with hand net of 0.5 mm mesh in three different 2 m × 1 m sampling points (20 m apart). Larvae were put in 70% ethanol and measured in the laboratory (body length without caudal lamellae and head width) with a digital caliper to the nearest 0.01 mm. Only the five last larval stadia were taken into account in further analyses of larval growth. Smaller stadia were found only in January and February and their omission does not influence our conclusions on the pattern of larval development. These stadia were identified using morphological characteristics including head width, number of segments covered by wing sheaths, and prementum (Khelifa R., unpublished data).

### ***Flight season, lifespan, and maturation***

During our daily visits, the dates of the first observed imago and reproductive pair were recorded to determine the start of the flight and reproductive season, respectively. Given that the flight period of the species is long (from May to October; Dijkstra & Lewington, 2007), we could not carry out daily records of individuals to determine the peak number of adults and the end of flight season. To get approximate estimates of the latter parameters, the numbers of males and females were recorded twice a month (in the second and fourth week of the month) at 12:00 within a transect of 200 m of the watercourse. The counts of adults were conducted only when the weather conditions were good (no rain and no clouds).

In a parallel study that was carried out during the same flight season, adults were individually marked with permanent markers on one of the hind wings with numeric codes and

recaptured daily afterwards. To estimate the maturation period, we took information of capture-mark-recapture from individuals that were first captured as teneral and that were later recorded as reproducers. The estimated maturation period as the minimum period observed among those individuals. We considered the minimum rather than the mean maturation period because we assume that the long observed maturation periods were due to the non-detection of individuals. Lifespan was calculated by adding the estimated age of the first capture (using coloration pattern) to the number of days between the first capture and last recapture.

### Statistical analyses

Statistical analyses were performed with the software R 3.0.1 (R Development Core Team, 2014). A chi-squared test was carried out to see whether the frequency distribution of the five last larval stadia changes during the winter (December to February). A simple chi-squared test was carried out to check whether the proportion of males at emergence was equal to that of females. In order to test the difference of exuvia body length between males and females, a Mann–Whitney–Wilcoxon test was conducted. To check for seasonal pattern in body size of exuviae, multiple linear regressions was carried out with body length as response variable and season and sex as explanatory variables. Values are mean  $\pm$  SD.

## Results

### Embryonic development

Air temperature in the laboratory showed low daily variation with a mean of  $27.08 \pm 1.34^\circ\text{C}$  (Figure 1). The analysis of embryonic development is based on 1059 eggs collected from nine

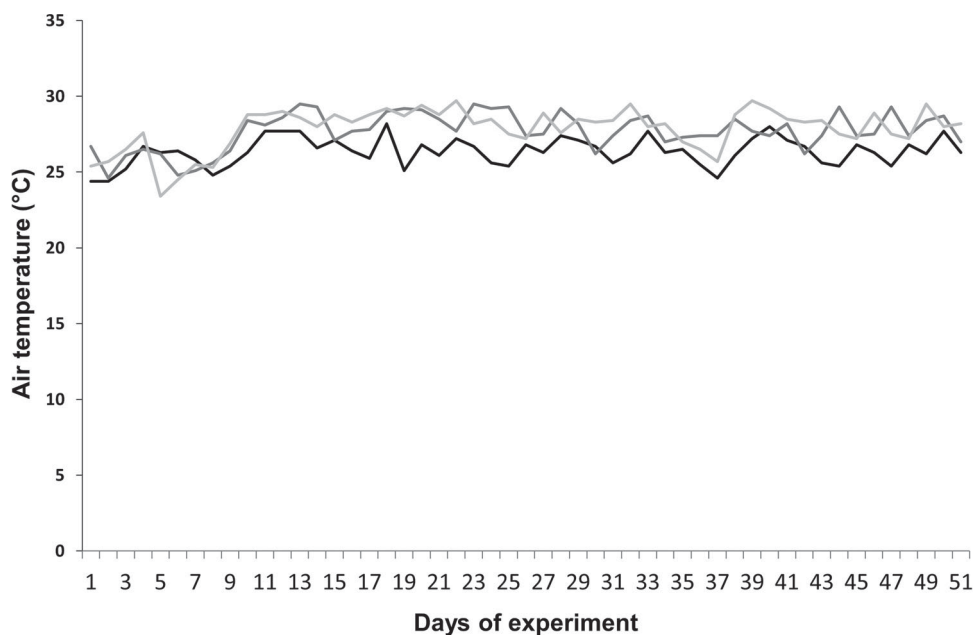


Figure 1. Air temperature of the laboratory during the survey of embryonic development. Black, dark grey and light grey refer to morning (09:00), afternoon (14:00) and evening (20:00), respectively.

Table 1. Egg sampling and hatching success in *Platynemesis subdilatata* during the laboratory experiment.

Female	Date	Number of eggs collected	Number of eggs hatched	Hatching success (%)
1	18 June 2012	72	61	84.7
2	18 June 2012	152	125	82.2
3	18 June 2012	98	29	29.6
4	20 June 2012	35	33	94.3
5	20 June 2012	151	33	21.9
6	22 June 2012	177	129	72.9
7	22 June 2012	137	61	44.5
8	22 June 2012	165	43	26.1
9	22 June 2012	72	3	4.2

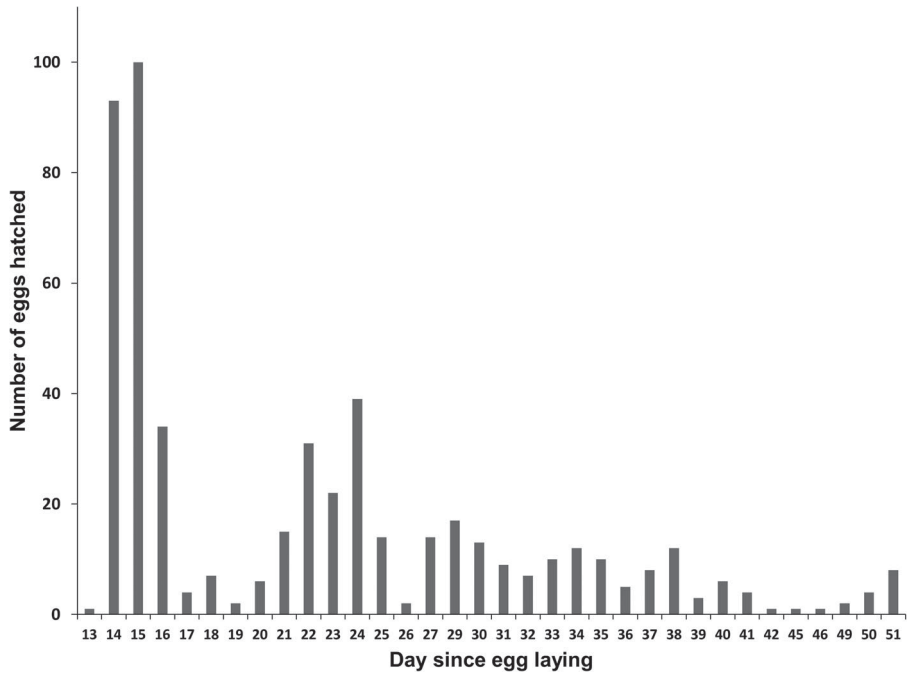


Figure 2. Pattern of embryonic development of *Platynemesis subdilatata* under laboratory conditions.

different females. Only 517 eggs hatched, which gives a hatching success of 48.8%. Infertility was recorded in 154 eggs (14.5%). The cause of unhatchability of 388 eggs (36.7%) was undetermined. The hatching success varied from 4.2% to 94.3% among females (Table 1). There was high variability in the duration of embryonic development among eggs (Figure 2). The earliest and latest hatchings took place after 13 and 51 days of egg laying, respectively. Figure 2 shows a high positive skew in the distribution of egg hatching over time. The peak of hatching was recorded on days 14 and 15, which, combined, represent 37.3% of all hatched eggs. The time after which 50% of eggs hatched was 21 days from egg deposition and nine days from the first hatching.

### Larval growth

The analysis of larval population structure was based on 148 larvae collected monthly from December to June. Figure 3 presents the frequency distribution of the five last larval stadia. This

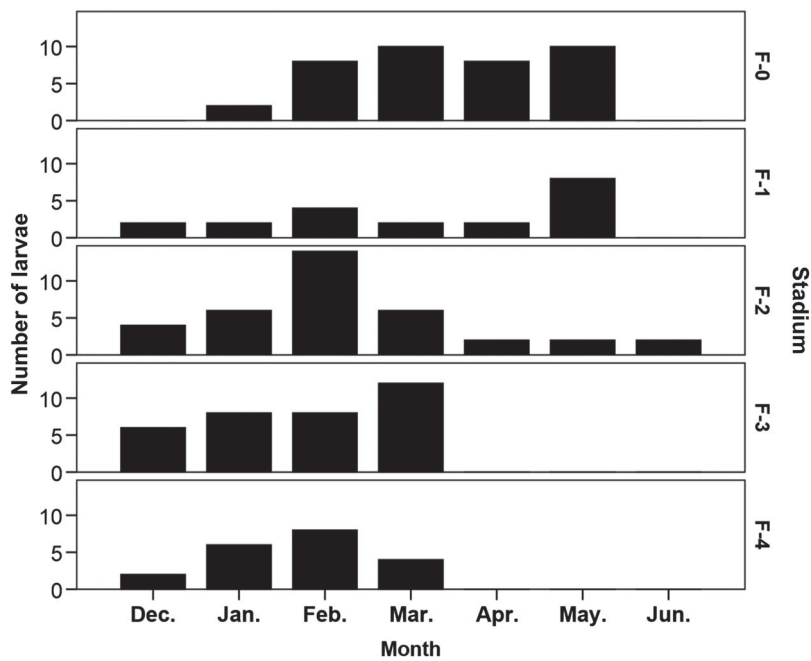


Figure 3. Frequency distribution of the five last larval stadia of *Platycnemis subdilataa*.

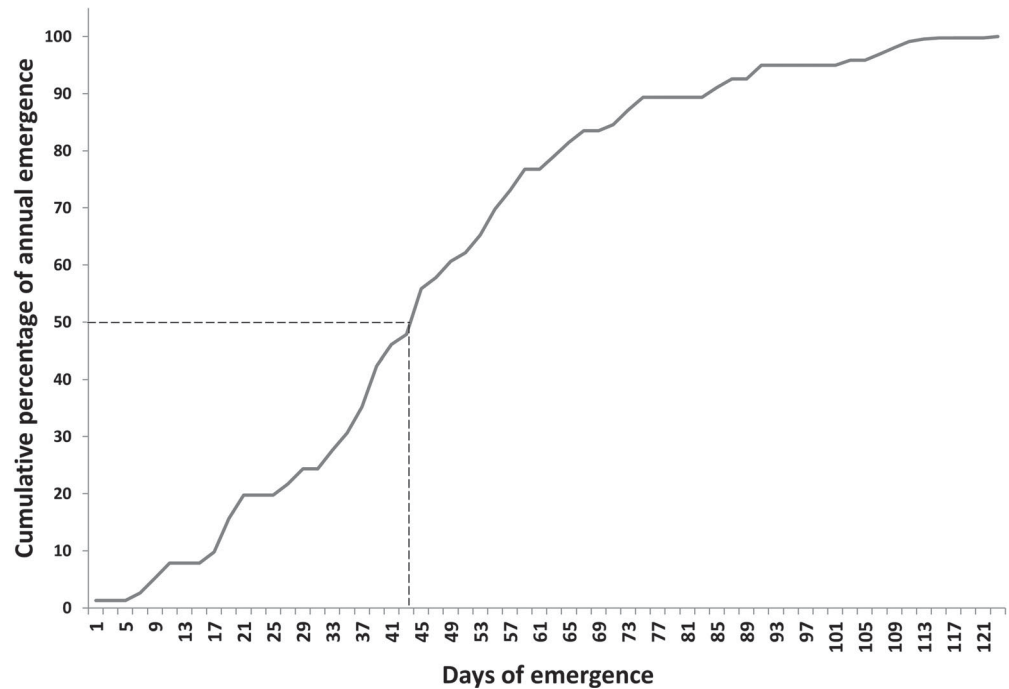


Figure 4. Emergence pattern of *Platycnemis subdilataa* in the study site. Dashed lines indicate the time at which 50% of the annual population emerges.

frequency changed significantly during the winter (January–February; Pearson’s chi-squared test:  $\chi^2 = 64.12$ ,  $df = 24$ ,  $p < 0.0001$ ); a period during which the five last stadia were recorded. From December to February, the percentage of F-2 and F-3 combined represented 71.4%, 58.3% and 52.3%, respectively. The proportion of F-0 increased from 0 in December to 19.0% in February. Prior to emergence (late April), the larval population consisted of two thirds of F-0 and one sixth of both F-1 and F-2. No larvae were recorded in July.

*Temporal pattern of emergence*

A total of 460 exuviae were collected during 122 days of emergence (Figure 4). The first and last exuviae were recorded on 8 May and 7 August. The number of exuviae peaked in mid-June. EM50 was 44 days in both sexes. Sex ratio was slightly but not significantly female biased (50.65%,  $\chi^2 = 0.07$ ,  $p = 0.77$ ).

Exuvia body length was significantly larger in females ( $11.65 \pm 0.82$  mm) than males ( $11.18 \pm 0.92$  mm) (Wilcoxon test:  $p < 0.0001$ ). There was a seasonal decline in body length (Table 2, Figure 5), and the slope of the regression of body length over the emergence season was similar in both sexes.

*Flight season, lifespan and maturation*

The flight season of *P. subdilatata* lasted 133 days; the first recorded individuals were on 4 May whereas the last imagos were observed on 14 September. Figure 6 presents bimonthly counts

Table 2. Summary results of multiple linear regression of body length pattern of exuviae of both sexes over the emergence season of *Platycnemis subdilatata*. Multiple R-squared: 0.151.

	Estimate	Standard error	t-value	p-value
Intercept	13.541	0.3061	44.232	< 0.0001
Julian date	− 0.0108	0.0017	− 6.286	< 0.0001
Sex [male]	− 0.476	0.0861	− 5.536	< 0.0001

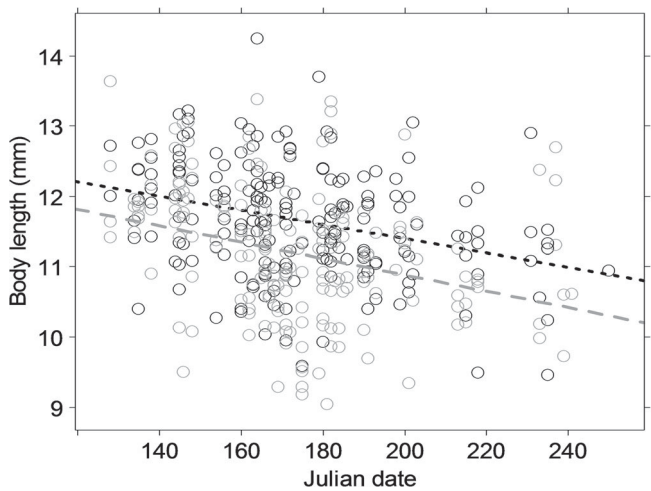


Figure 5. Seasonal pattern of body length of *Platycnemis subdilatata* exuviae. Black and grey represent females and males, respectively. Dashed lines are regression lines.

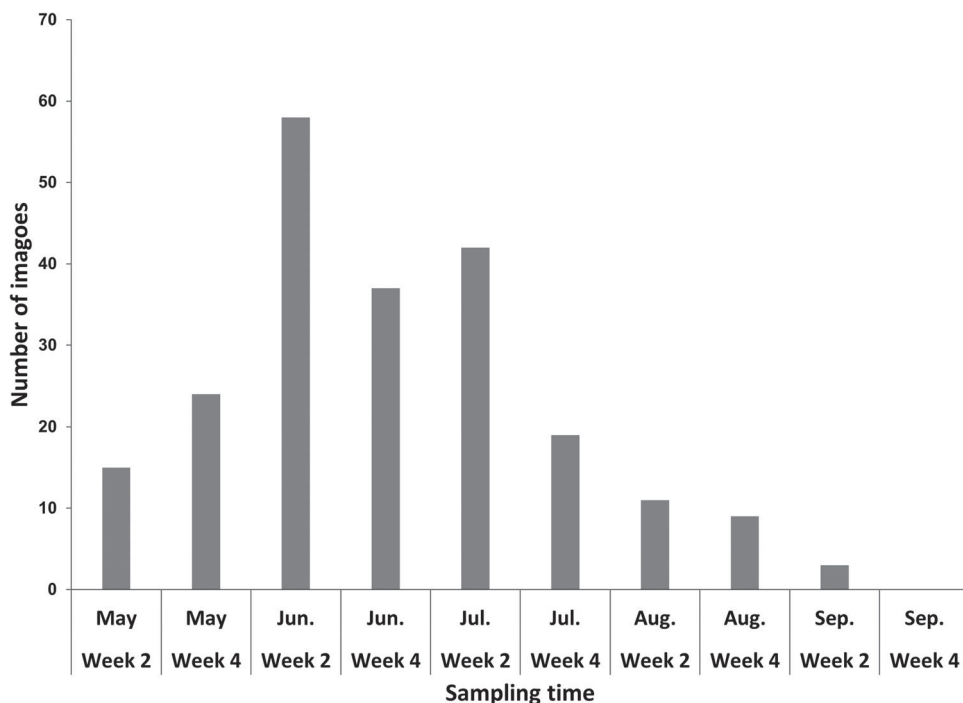


Figure 6. Bimonthly counts of *Platynemesis subdilatata* imagoes in the study site. Counts were carried out during the second and fourth weeks of the month.

of imagoes during the flight season. The number of imagoes peaked in the first half of June. The reproductive season started five days after the first recorded individual.

There was no significant difference between the lifespan of males ( $7.85 \pm 6.91$  days,  $n = 462$ ) and females ( $7.66 \pm 5.97$  days,  $n = 480$ ) (Wilcoxon rank sum test:  $W = 106010$ ,  $p = 0.24$ ), with a mean of  $7.75 \pm 6.45$  days. However, maximum lifespan was longer in males (48 days) than females (37 days). Males and females spent a maturation period of six and seven days, respectively.

## Discussion

The combination of data from embryonic development, larval growth, temporal pattern of emergence and flight period revealed that *P. subdilatata* is a univoltine species with asynchronous emergence and relatively long adult season.

The duration of egg hatching reveals that the species has direct embryonic development. This duration was highly variable, lasting 38 days from the first to the last hatching under laboratory air temperature of  $27.08 \pm 1.34^\circ\text{C}$ . Similar pattern was observed in *Pyrrosoma nymphula* in which the egg hatching lasted 34 days with temperature varying from 18 to  $24^\circ\text{C}$  (Bennett & Mill, 1995). Due to the fact that a relatively high proportion of eggs of *P. subdilatata* hatch synchronously during the first days, the general temporal pattern of egg hatching was positively skewed. Such a skew was also observed in *P. nymphula* (Bennett & Mill, 1995) and *Urothemis edwardsii* (Khelifa et al., 2013). The hatching success (48.8%) was lower than most published studies (Corbet, 1999, p. 61), and one reason could be that the optimal oxygen requirements of eggs of this lotic species were not fully met in the laboratory, inducing high unhatchability (Woods & Hill, 2004).



Larval population structure was quite asynchronous before the winter and less so before emergence. During the winter, the five last larval stadia were recorded with F-2 and F-3 combined presenting more than 50% of the population. The occurrence of winter diapause was not probable since the proportion of F-0 increased from December to February. It is likely that winter water temperature in the study site did not go below a threshold that prevents larval development. In the same region, Mahdjoub et al. (2014) showed that *Coenagrion mercuriale* larvae do not show larval diapause and continue to develop slowly throughout the winter. The asynchrony in egg hatching may play a role in the asynchrony of larval population structure because early hatching reaches relatively advanced stadia when the last eggs of the year are hatching. However, the role of temporal pattern of egg hatching is only partial and other factors, e.g. female mature lifespan, might also determine larval population structure. In fact, considering that the maximum mature lifespan of *P. subdilatata* females was estimated to 30 days and one female may lay eggs sequentially over her lifespan, the first and last oviposition might take place a few weeks apart.

The asynchronous population structure of larvae has consequences on the temporal pattern of emergence, which in turn influences flight period (Corbet, 1999, p. 245). As expected from the frequency distribution of larval stadia, the emergence season was long and similar to that recorded in *P. pennipes* (95 days; Lehmann, 1994). Such a pattern is typical of summer species (Corbet, 1954). The EM50 of *P. subdilatata* is later than that recorded in many damselflies of temperate zones, e.g. *C. mercuriale* with 25 days in UK (Purse & Thompson, 2003) and 23 days in northeast Algeria (Mahdjoub et al., 2014), and *Coenagrion hastulatum* with 11 days in Germany (Befeld, Katur, Lepkojus, & Rolff, 1997). Moreover, sex ratio was close to the equilibrium (50.65%), similar to that found in *Lestes viridis* (51.6%) (Hoess, 1993) but different from the general pattern in zygopterans, being slightly male biased (Corbet & Hoess, 1998). The observed sex ratio suggests that both sexes had relatively the same mortality during egg and larval stages.

Body length decreased gradually over the season in both sexes, as recorded in *P. pennipes* (Lehmann, 1994) and many other odonates (e.g. Mahdjoub et al., 2014; Purse & Thompson, 2003). Although significant, the relationship between body length and season ( $R^2 = 0.151$ ) was weaker than that recorded in *C. mercuriale* in northeast Algeria ( $R^2 = 0.25$ ; Mahdjoub et al., 2015). Although Rowe and Ludwig (1991) proved that the seasonal decline of body size may have no relationship with temperature, we are of the opinion that temperature played an important role in shaping the seasonal pattern of body size, considering the long reproductive season and the asynchronous egg hatching of the species. In fact, taking into account the reproductive season and embryonic development estimated in the laboratory, early reproductive females lay eggs that hatch approximately in late May while late reproductive females lay eggs that may hatch in October. The former encounter warmer temperatures than the latter; this probably affects the growth and development rate of larvae, resulting in variability of body size at emergence.

The long flight season is due to the asynchronous emergence. The first observed adult was recorded four days before the first exuvia was sampled. This was due to the fact that emergence at the surveyed stretches started later than other parts of the stream. The first reproductive pairs were recorded five days after emergence, which is approximately consistent with the maturation period of six and seven days in females and males, respectively. Cordero-Rivera & Stoks (2008) reviewed the lifespan of adult odonates and estimated a mean of 7.6 days for zygopterans, which was similar to the lifespan estimated in *P. subdilatata* in this study. However, Aguesse (1961) presented a mean lifespan of 5.8 days and 6.2 days for *P. acutipennis* males and females, respectively, which is slightly shorter than that of *P. subdilatata*. Considering the larval population structure, emergence pattern and flight period, it is less likely that the species produce more than one generation per year in the study site. However, it is probable that other populations living in warmer sites with higher food availability might present at least partial bivoltinism.

Our study presents new data on the life cycle of *Platycnemis subdilatata*, providing information about its seasonal regulation in the eastern part of its range. It is important to determine how life cycle varies across the species range, and the environmental factors (abiotic and biotic) that shape the seasonal regulation. Since the species is widespread in watersheds (e.g. Khelifa et al., 2011), it is crucial to investigate the gradient of larval development and emergence pattern from upstream to downstream.

## Acknowledgments

We thank two anonymous referees for their useful comments and suggestions. We are thankful to Amin Kahalerras for field assistance. Thanks to Hichem Amari for exuvia measurements.

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